A SYNOPSIS OF THE WEST INDIAN LYCAENIDAE, WITH REMARKS ON THEIR ZOOGEOGRAPHY

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THE BASIC REFERENCE for students of the Antillean Lycaenidae is the thorough revision of Comstock & Huntington (1943). The particular strength of this work is in the detail at species and subspecies level, in the very large amount of material so profitably studied that few major subsequent distributional discoveries have been or are likely to be made, and in the meticulous and extremely perceptive study of the older literature that underlies the whole work, resulting in a stability of species nomenclature that many a better known area might well envy.

Problems of higher classification in the family, however, were almost completely passed over. Reason for this is not hard to discover: the problems involved so far transcended the boundaries of the West Indies that to resolve them would have necessitated an effort out of all proportion to the study and very likely would have greatly postponed or even completely stopped its appearance.

Subsequent work by others now has made considerable progress in reducing that hiatus. Of particular significance is the revision of some of the blues by Nabokov (1945), who brought an intimate knowledge of palearctic as well as nearctic groups to bear on the neotropical fauna, where this knowledge was peculiarly valuable. Much later my own work on the reclassification of the North American hairstreaks (Clench, 1961) touched on many West Indian groups and indicated that the male genitalia in particular could be of major assistance in determining their relationships.

Some time ago Mr. F. Martin Brown asked if I would go over the Jamaican hairstreaks for him in order to bring their generic classification into line with the North American revision. This took more time than at first expected, particularly in the collateral examination of mainland species, but when the task was done it was evident that a very little additional work would extend the results from just one island to the whole West Indian region. In view of the many changes indicated by Nabokov's work and of an unpublished survey of my own of *Leptotes* (world-wide), prepared by a fortunate coincidence for quite another purpose, it seemed opportune to combine all this into a synoptic list, herewith presented (Table I).

TABLE 1

SYNOPSIS OF THE WEST INDIAN LYCAENIDAE

family L Y C A E N I D A E
subfamily S T R Y M O N I N A E
tribe E U M A E I N I

    Eumaeus Hübner 1819
        1. atala Poey 1832 (Cuba, Bahamas ⚹)
            a. florida Rober 1926(Florida)
                =grayi Comstock and Huntington 1943

tribe S T R Y M O N I N I

    Chlorostrymon Clench 1961
        2. maesites Herrich-Schäffer (Florida, Bahamas,
            Cuba, Jamaica, Puerto Rico[not yet taken on
            Hispaniola but should occur])
            a. clenchi Comstock and Huntington 1943 (Dominica)
        3. simaethis Drury 1770 (Cuba, Hispaniola, Puerto
            Rico, Virgin Islands, St. Kitts, Dominica, St. Vincent)
            a. jago Comstock and Huntington 1943 (Jamaica)
            Other subspecies in Central and South America
    Calycopis Scudder 1876
        4. beon Cramer 1780 (Hispaniola). Status uncertain
    Nesiostrymon new genus (see note no. 1)
        5. celida Lucas 1957 (Cuba)
            a. shoumatoffi Comstock and Huntington 1943 (Jamaica)
            b. aibonito Comstock and Huntington 1943 (Puerto Rico)
            [not recorded from Hispaniola but probably occurs there]
    Callophrys Billberg 1820 ("see note no. 2")
        subgenus Cyanophrys Clench 1961
        6. crethona Hewitson 1873 (Jamaica)
    Pseudolycaena Wallengren 1859 (see note no. 3)
        7. marsyas Linnaeus 1758 (South America)
            a. cybele Godman and Salvin 1896 (St. Vincent)
            Another subspecies in South America
    Heterosmaitia new genus (see note no. 4)
        8. bourkei Kaye 1924 (Jamaica)
    Allosmaitia new genus (see note no. 5)
        9. coelebs Herrich-Schaffer 1862 (Cuba)
        10. fidena Hewitson 1867 (Hispaniola, Puerto Rico)
      ⚹ 11. piplea Godman and Salvin 1896 (St. Vincent, Grenada,
            Dominica)
    Strymon Hübner 1818
        12. acis Drury 1770 (Antigua Dominica ⚹)
            a. mars Fabricius 1777 (Puerto Rico,⚹Virgin Is., St. Kitts)
            b. petioni Comstock and Huntington 1943 (Hispaniola)
            c. casasi Comstock and Huntington (Cuba)
            Carpenter and Lewis (1943) report two subspecies from the Cayman Is.,
            one from Grand Cayman and one from Little Cayman and Cayman Brac.
            The identity of neither is known to me.
            d. armouri Clench 1943 (Bahamas)
            e. subspecies? (Caicos Islands: Rindge 1955)

          f. gossei Comstock and Huntington 1943 (Jamaica)

          g. bartrami Comstock and Huntington 1943 (Florida)

13. martialis Herrich-Schaffer 1864 (Florida; Bahamas; Cuba; Jamaica; Little Cayman, Cayman Islands)

14. rufofusca Hewitson 1877 (St. Vincent; [Central America])

15. bubastus Cramer 1780 [South America, including Trinidad]

          a. ponce Comstock and Hintington 1943 (Puerto Rico; Virgin Islands; St. Kitts; Antigua; Dominica; St. Lucia; St. Vincent; Grenada)

16. columella Fabricius 1793 (Hispaniola)

          a. modesta Maynard 1873 (Florida; Dry Tortugas *)

          b. cybira Hewitson 1874 (Jamaica; Cuba; Bahamas*, Grand Cayman, Cayman Islands *)

          c. arecibo Comstock and Huntington 1943 (Puerto Rico)

          Other subspecies in Central America and related islands.

* 17. antigua Comstock and Huntington 1943 (Antigua, Virgin Islands)

* 18. toussainti Comstock and Huntington 1943 (Hispaniola)

* 19. cristophei Comstock and Huntington 1943 (Hispaniola)

* 20. limenia Hewitson 1868 (Cuba; Jamaica; Hispaniola; Puerto Rico)

21. bazochii Godart 1822 [Central and South America]

          a. gundlachianus Bates 1935 (Cuba; Jamaica; Hispaniola)

Electrostrymon Clench 1961 (see note no. 6)

22. pan Drury 1773 (Jamaica)

23. angelia Hewitson 1874 (Cuba)

          a. pantoni Comstock and Huntington 1943 (Jamaica)

          b. dowi Clench 1941 (Bahamas)

          c. boyeri Comstock and Huntington 1943 (Hispaniola; Puerto Rico; Virgin Islands -St. Croix, 4. v. 1941, leg. Beatty: 2 males, Carnegie Museum)

24. angerona Godman and Salvin 1896 (St. Kitts; St. Vincent; Dominica)

* 25. dominicana Lathy 1904 (Dominica)

subfamily PLEBEJINAE

tribe CATOCHRYSOPINI

Leptotes Scudder 1876 (see note no. 7)

     (a) cassius group

26. cassius Cramer 1775 ([South America]; possibly Martinique)

          a. catilina Fabricius 1793 (Virgin Islands; St. Kitts)

          b. theonus Lucas 1857 (Florida; Bahamas; Cuba; Grand Cayman, Little Cayman and Cayman Brac, Cayman Islands; Jamaica; Hispaniola; Puerto Rico)

          c. chadwicki Comstock and Huntington 1943 (Dominica; Gaudeloupe)

          Other subspecies in Central America.

     (b) marina group

?27. marina Reakirt 1868 (Puerto Rico, probably as casual or misidentified theonus; [Central America])

28. perkinsae Kaye 1931 (Jamaica)

tribe P L E B E J I N I (see note no. 8)

Hemiargus Hübner 1818
  subgenus H e m i a r g u s Hübner 1818
    29. c e r a u n u s Fabricius 1793 (Jamaica; Hispaniola;
        Navassa)
        a. f i l e n u s Poey 1832 (Cuba; Bahamas; Grand Cayman,
           Cayman Islands ✶)
        b. a n t i b u b a s t u s Hübner 1818 (Florida; Georgia; etc.)
        Other subspecies in Central America, south to Costa Rica.
    30. h a n n o Stoll 1790 [South America, north to Costa Rica]
        a. w a t s o n i Comstock and Huntington 1943 (Hispaniola;
           Puerto Rico; Virgin Islands; St. Kitts; Antigua;
           Guadeloupe; Dominica; Martinique; St. Lucia; Grenada;
           Barbados)
        Other subspecies in South America.
  subgenus E c h i n a r g u s Nabokov 1945
    31. i s o l a Reakirt 1866 (Puerto Rico, probably casual;
        [Mexico])
        Other subspecies on the mainland, from western United
        States to Costa Rica.
  subgenus C y c l a r g u s Nabokov 1945 (see note no. 9)
    32. d o m i n i c a Moschler 1886 (Jamaica)
    33. a m m o n Lucas 1857 (Cuba; Bahamas; Grand Cayman,
        Cayman Islands)
    34. w o o d r u f f i Comstock and Huntington 1943 (Puerto Rico;
        Virgin Islands; St. Kitts)
    35. e r e m b i s Nabokov 1948 (Little Cayman Island, Cayman
        Brac, Cayman Islands)
    36. t h o m a s i Clench 1941 (Bahamas)
        a. b a h a m e n s i s Clench 1943 (Crooked Island, Bahamas,
           where it appears to be constant)
        b. b e t h u n e - b a k e r i Comstock and Huntington 1943
           (Florida)

        c. n o e l i Comstock and Huntington 1943 (Hispaniola; Mona
           Island)

Pseudochrysops Nabokov 1945
    37. b o r n o i Comstock and Huntington 1943 (Hispaniola;
        Puerto Rico [casual ?])

subfamily B R E P H I D I I N A E

Brephidium Scudder 1876 (see note no. 10)
    38. e x i l i s Boisduval 1852 [western United States through
        Central America]
        a. i s o p h t h a l m a Herrich-Schaffer 1862 (Bahamas;
           Cuba; Hispaniola; Jamaica; Grand Cayman, Cayman
           Islands)
           ⹀t h o m p s o n i Carpenter and Lewis 1943

  ✶ 39. b a r b o u r i Clench 1943 (Bahamas) Status uncertain
    40. p s e u d o f e a Morrison 1873 (Florida; Georgia; northern
        Bahamas)

All taxonomic changes and additions are provided in a series of notes referring to this list (Table I). The format of the list needs but few remarks. References are not given but may be obtained readily from Comstock & Huntington (1943) or some other work listed at the end. Distributions are complete so far as I know them. Species with an asterisk preceding their number have not been examined genitalically; all others have. An asterisk immediately following a locality indicates that the taxonomic status of the form in question is uncertain on the island.

Bates (1935: 188) remarked concerning the West Indian Lycaenidae, "The family at present, then, is of almost no use to . . . the zoögeographer," a remark which was certainly true enough when it was written. Comstock & Huntington's work made a considerable improvement, but left continental relationships, as before, quite uncertain. Nabokov's work and the present reclassification of the hairstreaks have both paid particular attention to these continental affinities, and as a result there are few forms whose relationship to mainland species or groups is still doubtful. The time, in other words, has come for a zoogeographic assessment of the group. For a number of reasons it has been impossible to attempt a "complete" analysis of Antillean lycaenid zoogeography. Instead, I have selected certain aspects of the problem for study and presentation here, and these may be found at the conclusion of the paper.

I. Nesiostrymon, new genus

Type species: *Thecla celida* Lucas 1857
(ssp. *shoumatoffi* Comstock & Huntington 1943)

Hind wing tailed. Male fore wing with a diffuse scent patch, its scales peripherally intermixed with ground color scales. Frons with appressed scales only, lacking any erect, bristle-like scales. Eyes with sparse, short hair. Male genitalia (fig. 3): the whole genital ring dorso-ventrally attenuate, due apparently to the ring being inclined (dorsal part to the rear) more than usual, relative to the body axis; falces of normal size, the fore arm straight with a slight, short, gradual apical constriction; an abrupt angle at the elbow; vinculum slender, sides subparallel for much of its length; saccus long, tapering, slender, with a rounded, slightly inflated tip; valvae short (considerably shorter, even, than the fore arm of the falx), completely fused with only a slight apical notch to indicate the division, broadest half-way from base. Penis long and slender, as usual, apically upcurving, with a single, simple exserted, acuminate cornutus, lightly sclerotized; no ventral terminal keel or ventral (or other exterior) teeth.

Remarks. Clearly related to *Ministrymon* Clench (*leda* Edwards, *clytie* Edwards) and to *Tmolus* Hübner (*echion* Linnaeus, *azia* Hewitson), although well differentiated from both. It may be distinguished from these two by the lack of bristly scaling on the frons, the more inclined genital ring and the consequent attenuation of this ring dorso-ventrally, and in the very short, completely fused valvae. With both it shares the single, simple acuminate cornutus, lack of ventral keel on penis tip, the very long saccus and the rather angular form of the falces.

The brilliant blue above is more like *Tmolus* (*echion*) than *Ministrymon*, as is the slightly more rounded wing shape and the diffuse scent patch.

The mainland (Mexico) species *tera* Hewitson is quite possibly congeneric but has not yet been examined critically.

II.   Callophrys (Cyanophrys) crethona Hewitson

The genitalia of this species (fig. 1) indicate quite conclusively that it is a true *Cyanophrys*. Like the pattern, however, they suggest that *crethona* is more different from continental members of the subgenus than most of the latter are from each other, thus implying a relatively great age to the separation of *crethona*. Comstock & Huntington (1943: 123) state, however, that it is closely related to an undescribed species from Mt. Roraima, Brasil, a species I have not seen.

III.   Pseudolycaena Wallengren 1859

Type species: *Papilio marsyas* Linnaeus 1758

Hind wing tailed, and with a tornal cleft. No scent patches. Frons with appressed scales only, lacking any erect bristle-like scaling. Eyes with sparse, short hair. Male genitalia (fig. 2): large, lateral hair pencils present, and a dorsal chitinous piece of undetermined shape attached to anterior border of tegumen; vinculum with posterior "shoulder" projection, vinculum strut prominent, strongly curved into this projection; falces rather strongly and evenly curved; saccus eight to ten times as long as width at middle, the sides subparallel, apex short, tapered, blunt; valvae rather short, broad, with lateral denticulate wings, pointed apex, slight dorso-lateral tooth, mesial borders divergent from before the middle. Penis with tip flared, definitely upturned, with two terminal cornuti, the longer one with small, obscure, apical teeth; terminal part of penis shaft with several short, external, longitudinal rows of small teeth.

Remarks. Structurally the genus is allied to *Atlides* Hübner (*halesus* Cramer) and *Arcas* Hübner (*imperialis* Cramer), particularly the former. All three of these genera share such significant characters as the extremely long, slender saccus, compact valvae, apically flared and upturned penis, special structural attachments on the anterior vinculum associated with the lateral hair pencils; and all three have the curious and interesting tornal cleft on the hind wing, as first pointed out by Godman & Salvin (1887: 15).

So far as I know the genus is monotypic, the sole species, *marsyas* Linn., with a Central American subspecies (*damo* Druce), a South American (nominate *marsyas*) and the still little known Lesser Antillean subspecies, *cybele* Godm. & Salv.

Fig. 1. *Callophrys (Cyanophrys) crethona* Hewitson, male genitalia (slide C-705). Penis on left. This and the succeeding genitalia drawings were made from mounts prepared as follows: first the penis was removed; then the vinculum was cut through on the right side and the structures opened out so that the inner sufaces are uppermost. Drawings were made to show the complete structures of the left side only (though usually both valvae are drawn). Uncus, tegumen and falx are to the top right; saccus and valvae to the left. This somewhat unorthodox procedure permits showing the structures with a minimum amount of distortion.

Fig. 2. *Pseudolycaena m. marsyas* Linnaeus, male genitalia (slide C-822). Penis below, the central part of the shaft omitted, but with a scale to indicate true relative length.

Fig. 3. *Nesiostrymon celida shoumatoffi* Comstock & Huntington, male genitalia (slide C-708). Penis on left.

Fig. 4. *Heterosmaitia oppia* Godman & Salvin, male genitalia (slide C-823). Penis below.

Fig. 5. *Allosmaitia coelebs* Herrich-Schäffer, male genitalia (slide C-829). Penis on left.

Fig. 6. *Heterosmaitia bourkei* Kaye, male genitalia (slide C-709). Penis below.

Fig. 7. *Heterosmaitia brescia* Hewitson (?), male genitalia (slide C-826). Penis below.
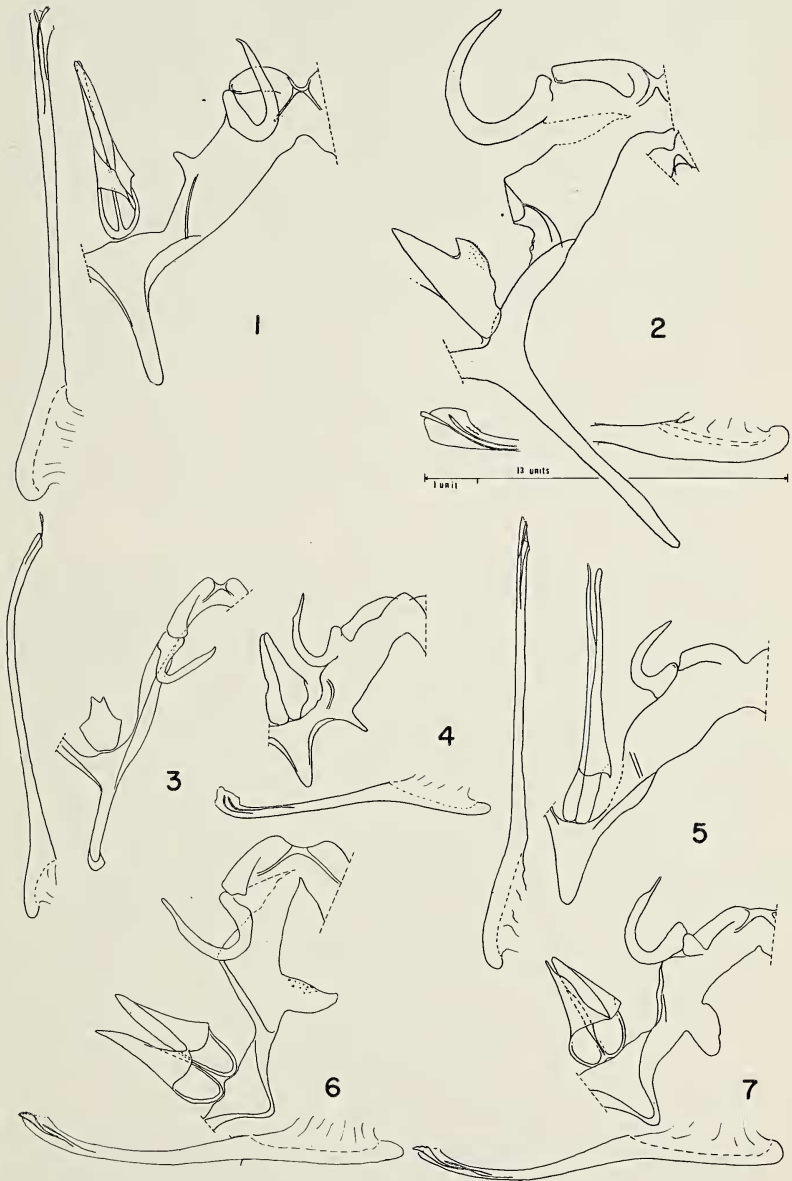
IV. Heterosmaitia, new genus

Type species: *Thecla bourkei* Kaye 1924 (Jamaica)

Hind wing tailed; males with androconial apparatus variable (see below). Frons bristled to variable degree. Male genitalia (Figs. 4, 6, 7): falces with tips prominently and abruptly constricted; vinculum with anterior triangular projection (associated with the paired lateral eversible scale tufts or coremata); saccus short, twice or less than twice as long as width at middle; valvae of normal length, simple, mesial edges smooth; penis without ventral keel or ventral teeth, more or less upturned apically, with two terminal cornuti. Males all with a tornal red spot on hind wing above.

Remarks. The genus is mostly developed on the mainland, principally in Central America. Investigation of potential relatives or possible members is still incomplete, but studied members may be grouped as follows:

1. *oppia* group

Eyes with dense, long hairs. Frons with dense, erect, long bristles in the median dark area; male fore wing without scent pad; hind wing with a dark glandular patch at origin of Rs, with a few long, erect, specialized scales from it near its posterior border; associated with this is a flat-lying, heavy fringe of dark scales arising on the inner margin of the fore wing below, directed anteriorly; around this fringe the wing scaling is modified to form a large opalescent-iridescent patch in Cu_2-2A below cell, with a patch of dark ochraceous mealy scales in the center. Male genitalia (fig. 4): anterior triangular process of vinculum small, close to saccus; valvae ventrally contiguous to near their tips; penis strongly upturned apically; cornuti subequal in thickness, with few or no apical teeth.

Includes only the Central American *oppia* Godman & Salvin.

2. *bourkei* group

Eyes with short, sparse hairs. Frons with bristles sparse, slight; male with scent pad on fore wing at cell-end; no specialized scaling on fore wing below or hind wing above. Male genitalia: anterior triangular process of vinculum large, farther from saccus (more or less mid-lateral); mesial edges of valvae divergent from before the middle; penis slightly upturned apically; one cornutus apically much thicker than the other with many apical teeth.

Subgroup A. Saccus much less than half as long as valva; larger cornutus with apical expanded part short, the expansion abrupt; penis slightly upturned (fig. 6). Subterminal line of fore wing below rather well developed; fuscous border of male fore wing above covers about half the cell-end-to-apex distance.

Includes *bourkei* Kaye (Jamaica) and at least two Central American species, one of which has been tentatively identified as *guadala* Schaus.

Subgroup B. Saccus much more than half as long as valva; large cornutus with apical expansion gradual and rather long; penis not at all upturned (fig. 7). Subterminal line of fore wing below very faint; fuscous border of male fore wing above covers about 1/3 the cell-end-to-apex distance.

Includes several apparently distinct species ranging from Mexico to South America, including one tentatively identified as *brescia* Hewitson. No West Indian species are known.

V. Allosmaitia, new genus

Type species: *Thecla coelebs* Herrich-Schäffer 1862 (Cuba)

Hind wing tailed. Eyes with rather long, dense hairs. Frons sparsely bristled. Male without scent pad on fore wing but on hind wing with a tuft of long, dark hairs arising from a small modified patch in the angle between Sc and the costal border of the cell; associated with this there is on the fore wing below a small, shining patch of modified scales on the inner marginal area, near which vein 2A is slightly enlarged and scaleless. Male

genitalia (fig. 5): no triangular process on anterior border of vinculum; falces with gradually tapering tips; valvae exceeding long and slender, the result of a greatly attentuated and produced terminal region, the mesial border serrate terminally; penis apically very slightly and gradually upturned, with two cornuti, one of which is distally enlarged, spatulate, and provided with a flat terminal edge armed with a row of low teeth; saccus moderate in length. Male above with no red spot at tornus. Fore wing of male with fuscous border extending basad to cell-end.

Remarks. Clearly allied to the preceding genus, *Heterosmaitia,* differing most notably in the long tuft of hairs on the hind wing androconial patch, the absence of an anterior process on the vinculum, the extraordinarily produced valvae, the spatulate, truncate cornutus, as well as in the absence of a tornal red spot on the male hind wing above.

Includes the following species: *pion* Godman & Salvin (Central America), *coelebs* Herrich-Schäffer (Cuba), *fidena* Hewitson (Hispaniola, Puerto Rico). In addition, the following species probably also belong but no specimens have been available for study: *piplea* Godman & Salvin (=*subobscura* Lathy ?) (St. Vincent, Grenada, Dominica), *panchaea* Hewitson (=*scoteia* Hewitson ?) (Amazonas, Minas Geraes).

VI.   Electrostrymon Clench 1961

The West Indian species (save *dominicana* Lathy, which I have not seen) are, according to both pattern and genitalia, more closely interrelated than any is to *endymion* of the mainland, the type species and the only mainland species I have so far investigated.

VII.   Leptotes Scudder 1876

This genus is holotropical in distribution, being known in the Old World chiefly under the name *Syntarucus* Butler 1900. The American species divide neatly, according to male genital characters, into three groups and additional, co-equal, groups occur in the Old World. None of these groups would seem to warrant being called even a subgenus. The three American groups are:

(1)   The *cassius* group. This includes only *cassius* (with all its subspecies) and a still undescribed species from the Colombian Andes.

(2)   The *marina* group. Comprises *marina* Reakirt, *perkinsae* Kaye and perhaps *parrhasioides* Wallengren from the Galapagos Islands. This group is also represented by a number of species in Africa, Madagascar and associated islands.

(3)   The *callanga* group. This is perhaps the most primitive group in the genus, and includes *callanga* Dyar, from the Peruvian Andes, and most surprisingly *webbianus* Brullé of the Canary Islands.

VIII.   Tribe PLEBEJINI

The classification here is essentially that of Nabokov (1945), with his subfamily Plebejinae demoted to a tribe, his relevant genera demoted to subgenera under *Hemiargus,* except for *Pseudochrysops,* which is distinct enough in every way to be accorded full generic status.

IX.   Subgenus Cyclargus

Nabokov groups these five species into two "superspecies": (1) comprising *dominica* and *ammon;* (2) comprising *thomasi, woodruffi, erembis.* Interesting confirmation exists in the sympatry (more or less) of *ammon* and *thomasi* in the Bahamas; and Nabokov suggests that *erembis* may eventually be found in Cuba, sympatric there with *ammon.*
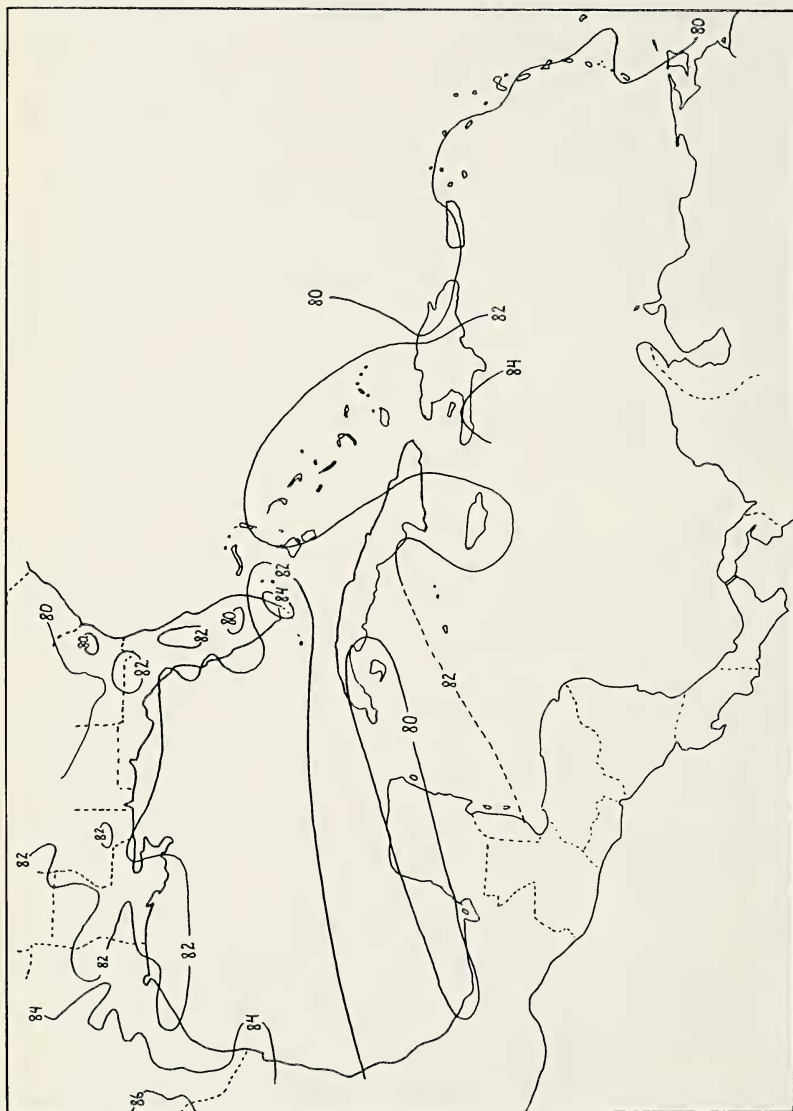
Fig. 8. Present-day mean July temperatures (°F) in the West Indies.

X. Brephidium Scudder 1870

Carpenter & Lewis (1943: 392) described *Brephidium isophthalma thompsoni* in comparison with *pseudofea* Morr., under the mistaken, but then prevalent, opinion that is was nominate *isophthalma*. It is not distinguishable from other Antillean populations of *isophthalma*.

Brephidium barbouri Clench was described as a distinct species, but later was synonymized by Gillham (1955). In view of Gillham's attitude towards subspecies, and of the subtle and minute species differences in the male genitalia of *Brephidium* which he may not have been able to appreciate, as well as of the differences given in the original description, his action must be restudied. Rindge's remarks (1955: 14) are interesting in this connection.

ZOOGEOGRAPHICAL CONSIDERATIONS

The general pattern of lycaenid distribution in the Antilles is essentially similar to that shown by most other groups of animals (cf. Darlington, 1957: 510). In brief, they constitute a depauperate fauna of distinctly Central American aspect; they can be entirely accounted for under an assumption of waif dispersal across water gaps similar to those occurring today; the most striking endemics of the region occur in Jamaica and Hispaniola; and despite the frequent development of endemic subspecies in the different islands or island groups the insular region as a whole presents a rather uniform, cohesive, facies. In contrast to some animal groups, however, the lycaenids of both southern Florida and the Lesser Antilles contain such a sizable and unmistakable West Indian component that for purposes of discussion these areas must be considered integral, if peripheral, parts of the Antillean region.

The following discussion is not intended to be a full analysis of West Indian lycaenid zoogeography. I have simply singled out for discussion a few points that seem especially clear or particularly interesting with emphasis on processes and events in the hope and belief that these are of the most interest and value to others.

1. Late Pleistocene climatic changes

If there is one event that stands out more than any other as the most important architect of the present distribution pattern of lycaenids in the West Indies, that event would have to be the last (Wisconsin) glaciation of the Pleistocene. It is well known, though still too little appreciated by some zoogeographers, that during the times of glacial advance temperatures dropped considerably not just at the ice front but the world over. The actual amount of the drop undoubtedly varied to some extent from place to place but it was on the order of approximately 9° Fahrenheit (Flint, 1947: 455). Antillean lycaenids demonstrate such a temperature drop quite unmistakably, and even indicate certain of its details. Since summer temperatures in the West Indies (fig. 8) are very little zoned there is no direct evidence in the lycaenids whether or not these temperatures were affected by Wisconsin cooling[3]

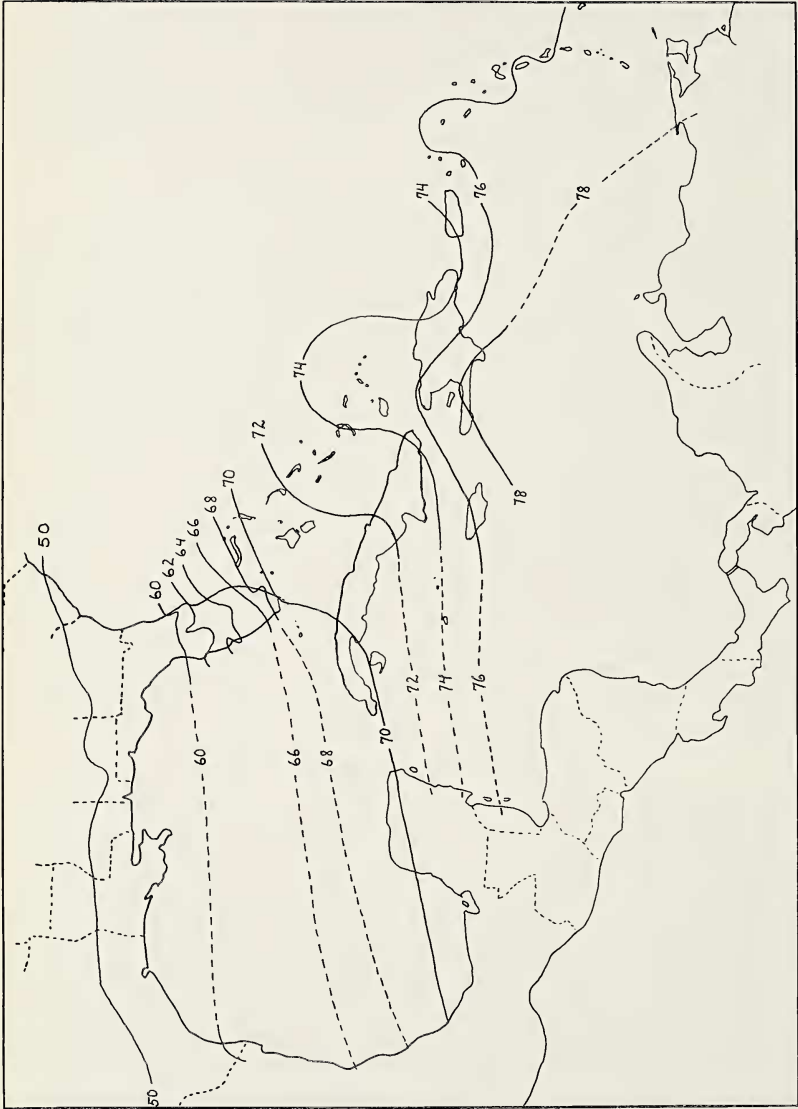[3]Though a certain amount of indirect evidence suggests that they probably were.

Fig. 9. Present-day mean January temperatures (°F) in the West Indies.

but there is definite indication that winter temperatures were lowered. The amount of winter (January) mean temperature reduction that best fits the present distributional evidence is approximately 8° F. Interestingly only a very slight modification of the present January isotherm contours (fig. 9) is required: a uniform reduction would almost suffice. The needed modification is a slight shift to the east of the "warm zone" which now lies over western Hispaniola, and of the cooler zone which occurs just to the east over northeastern Hispaniola and western Puerto Rico, so that the first would lie squarely over Hispaniola and the second directly over Puerto Rico.

The evidence that leads to these conclusions consists of three parts: (1) evidence for the reduction and its amount; (2) evidence for the slight eastward zonal shift; and (3) evidence for the time when this happened.

The reduction and its amount. Let us begin with the Antillean element in peninsular Florida, which is clear-cut, of obvious derivation (Cuba or the Bahamas) and, most importantly, is "open ended" — the northern limits of the ranges are determined by the direct interaction of the organisms and the environment, rather than being imposed by an island shore.

Florida's Antillean lycaenids may be divided into three groups according to their relationships to their nearest relatives in the islands:

  Ia. Undifferentiated. *Chlorostrymon maesites, Strymon martialis, Leptotes cassius theonus.*
  Ib. Subspecifically distinct. *Eumaeus atala, Strymon acis, S. columella, Hemiargus thomasi, H. ceraunus.*
  Ic. Specifically distinct. Only *Brephidium pseudofea* (whose probably postglacial invasion of the northern Bahamas may be ignored for present purposes).

On the basis of their tolerance to January mean temperatures in Florida they also divide into three groups but diffeerntly assorted:

  IIa. Northern boundary coincides more or less with 65° isotherm: *E. atala, C. maesites, S. acis, S. martialis, S. columella.*
  IIb. Northern boundary coincides more or less with 62° isotherm: *L. cassius, H. thomasi.*
  IIc. Northern boundary farther north than 60° isotherm: *H. ceraunus, B. pseudofea.*

The hypothesis which best explains the above facts is that at some past time conditions in Florida were measurably cooler than now; that during this cooler time and because of it the greater part of the Antillean element was absent; and that subsequently conditions warmed to about their present state, permitting the island forms to invade the peninsula and establish themselves, creating the present fauna. Important in this connection is the degree of differentiation of these

invaders. This is discussed more fully below and all that need be said here is that with the exception of *pseudofea* (Ic above) they show a fairly consistent degree of differentiation ("slight" subspecies to undifferentiated) of a small order of magnitude. This argues for a nearly simultaneous entry into Florida not very long ago (as opposed, for example, to random arrival and establishment at intervals over a long period of time.)

A drop of twenty degrees would be required to completely elim- inate all the West Indian species now in Florida because of the con- siderably more cool tolerant group IIc above. Such a reduction is patently absurd for it would also have eliminated virtually all the lycaenids in the islands too. A much more realistic 8° would suffice to lower the mean January temperature of warmest Florida from its 70° to 62°, probably sufficient to wipe out all but the rebellious IIc species and further south not too severe for survival on some islands. Taking into consideration the distinct possibility that some species, particularly those of group IIb, may have become adapted in Florida to somewhat cooler conditions than they could tolerate when they first arrived (for several reasons more likely on the mainland than in the islands), a more conservative 6° might be suggested. The higher figure, however, is preferable because of what apparently happened in the islands: a drop of only 6° would be insufficient to explain the pattern of survival which is indicated there (discussed more fully be- low). Nonetheless this reasoning suggests that in the absence of the stronger selection pressures of the mainland the minimum tolerance of Antillean lycaenids was about 66° mean January temperature.

The eastward zonal shift. A reduction of 8° in the present Antillean January isotherm of 74° would bring it down to the suggested critical value of 66°, and this isotherm may be imagined as roughly dividing the insular region into two areas: a northern one which in Wisconsin time had winter temperatures below the critical value; and a southern one which had temperatures above this value and hence presumably could have served as a refuge area during that glaciation.

An island which today harbors one or more endemic full species can be presumed to have maintained at least those species through Wisconsin times. Jamaica has five such endemics, Hispaniola three, Cuba three (including *E. atala* which, though not endemic, must have survived the glaciation there). Puerto Rico and the Bahamas have none. There are also several significant endemics in the Lesser An- tilles, but distributional knowledge is insufficient to discuss them in detail. It is legitimate to conclude from this that Jamaica, Hispaniola, and the Lesser Antilles must have had adequate winter temperatures during Wisconsin time while Puerto Rico and the Bahamas did not. Cuba, on this basis, probably had adequate conditions but only marg- inally so.

The present January isotherm of 74° (hypothetical Wisconsin 66°) comes close to dividing the Antilles in just that way. It passes barely through southernmost Cuba, consistent with the marginal conditions just suggested; Jamaica and the Lesser Antilles lie wholly below it and Hispaniola nearly so, in harmony with the conditions suggested by their relatively large number of endemics.

But as it stands it is not perfect. Marginal conditions, according to the present configuration of the isotherm, should have prevailed in the southern Bahamas and in Puerto Rico, whereas there is no evidence that any lycaenids survived in either. Adjustment of the configuration to conform with the endemics (and lack thereof) is, however, minor: push it southward where it intersects the Bahamas[4] and nudge it a little to the east where it crosses Hispaniola and back again over Puerto Rico. The results are shown in fig. 10.

The time it happened. The best source of information on this point is the degree of differentiation that has taken place between the forms in Florida and their nearest insular relatives (see groups Ia, Ib, above). The maximum differentiation is shown by the members of Ib, all of which are "slight" subspecies of insular species. This degree of divergence is typical of what is imputed to post-Wisconsin effects in many groups of animals (not just lycaenids, or even just butterflies), and in places where glacial influence is more directly ascribed to the differentiation. Little more need be said: by their degree of divergence, the concordance of several forms, and their presence in a place where conditions were appropriate, they indicate arrival in Florida, either from Cuba or the Bahamas, closely following the warming temperatures that accompanied recession of the Wisconsin ice sheet far to the north.

As to the undifferentiated species in group Ia, there are two explanations. They might be late arrivals and accordingly have had too little time to become differentiated; or they might have arrived with the others but because of a much lower evolution rate have simply failed to diverge. I incline to the latter possibility for a number of reasons:

First, these same species show similar effects among the islands: no divergence between islands where other species have become post-glacially divergent, sometimes (e.g. *C. maesites*) showing subspecies only where a separate glacial refuge can be invoked.

Second, when the temperatures were warming at the end of Wisconsin time the northerly islands must have presented a sort of ecological vacuum extremely receptive to immigrants from the south. Since then, however, it is likely that the hypothesized "closed association" or "closed community" effect has become operative. This hypothesis

[4]A little push only; a very few butterflies, *Eurema chamberlaini* Butler being the most conspicuous, seem to have been able to persist in these islands during the Wisconsin.
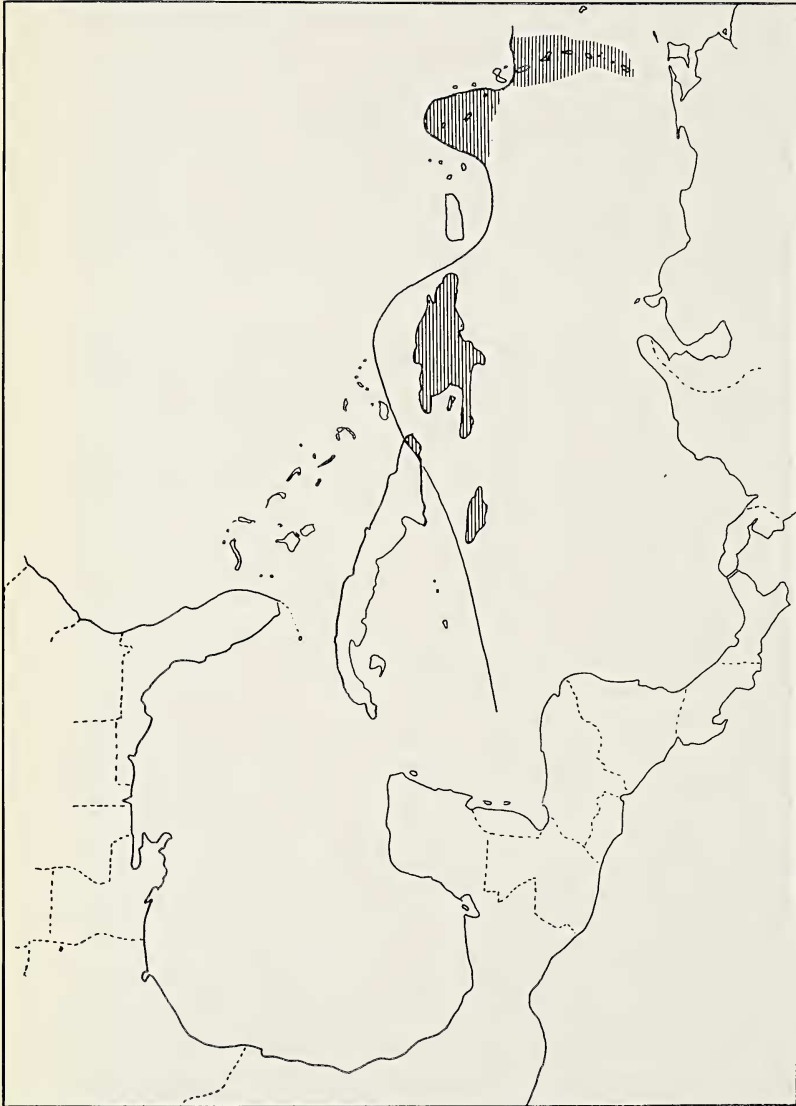
Fig. 10. Assumed mean conditions for January during Wisconcin glacial maximum. Line represents approximate position of 66°F isotherm (position and configuration based on present day January isotherm of 74° with modifications: see text). Shaded areas represent presumed refugia during Wisconsin time.

(cf. Weaver & Clements, 1938: 171) holds that in a climatically stable situation communities so adequately fill the available niches that they tend to impede the establishment of immigrants from without. It is, of course, not an absolute condition but a tendency. It must, however, become increasingly effective with decreasing distance from the prospective source of the immigrant. Between the West Indian islands, for example, it seems probable that movement between adjacent islands is sufficiently frequent that those forms capable of becoming established have already done so long ago while those incapable continue to fail.

Third, statistically it is more logical to expect a variety of evolution rates in a group than a single rate. There is no reason whatever to expect a form to subspeciate simply because it has the chance. Florida's Antillean lycaenids present an entirely reasonable pattern of some low rates, some higher rates (time has been insufficient to distinguish clearly between "high" and "not so high" rates, however).

Resumé. It would be well to recapitulate the events discussed above, putting them in chronological order.

(1) The advance of the Wisconsin ice sheet was accompanied all over the world by a marked drop in temperature. In the West Indies the effect was to reduce mean January temperatures by about 8°F., the effect, if any, on summer temperatures being indeterminate.

(2) The result of this was to extirpate completely the Antillean lycaenids in Florida (except *Brephidium pseudofea*), the Bahamas and Puerto Rico, and most of them in Cuba. Survival was possible on a large scale only in Jamaica, Hispaniola and in the Lesser Antilles (the latter discussed below).

(3) When the Wisconsin sheet retreated, some 12,000 years ago, conditions returned to approximately their present state and concurrently many species that had been confined to the three or four refugia just mentioned spread out rapidly, occupying all islands (more or less) capable of supporting them.

(4) Since that time certain of these species have evolved, or have continued to evolve, producing subspecific differentiation among the islands. Others with a slower evolution rate have remained visibly undifferentiated.

It may be of interest to summarize the probable or possible lycaenid faunal composition of the four principal refugia at the height of the Wisconsin glaciation. The evidence allocating a particular species to one or another refugium is various. Endemic full species are, of course, immediately assignable. But assignment of others is based on the most likely refugium, granted the foregoing sequence of events. Species that today show among the islands subspecies of about equal divergence one from another (e.g., the subspecies of *E. angelia*) are assumed to have spread out from a single refugium. Those such as *S. acis* that show two groups of subspecies suggest double refugia with subspeciation already in progress between them during Wisconsin time.

1.   Cuba. *E. atala, A. coelebs* and *H. ammon* are endemic there or nearly so, and apparently survived the Wisconsin there. A total of three species.

2.   Jamacia. *C. crethona, H. bourkei, E. pan, L. perkinsae* and *H. dominica* are all endemic full species and must have survived the Wisconsin *in situ*; in addition the following were likely: *S. acis* (ancestor of sspp. *bartrami, casasi, gossei, armouri*), *S. martialis, S. columella* (ancestor of sspp. *modesta, cybira*), *L. cassius theonus, H. ceraunus* (ancestor of sspp. *filenus, ceraunus, antibubastus*), *B. exilis isophthalma.* A total of 11 species listed.

3.   Hispaniola. *S. cristophei, S. toussainti, P. bornoi* are all endemic there today. Additionally the following were likely: *A. fidena, S. acis* ancestor of sspp. *acis, mars, petioni*) *S. columella* (ancestor of sspp. *columella, arecibo*), *S. limenia, E. angelia, H. thomasi.* A total of nine species listed.

4.   Lesser Antilles. *A. piplea, S. antigua, E. angerona, E. dominica* are all endemic there today. The following were likely in addition: *P. marsyas cybele, S. bubastus ponce, L. cassius catilina, L. cassius chadwicki, H. hanno watsoni, H. woodruffi.* A total of nine species listed, one of them in two subspecies.

The following species were undoubtedly present on one or more of these refugia but the particular one (or ones) cannot now be deducted from available data: *N. celida; S. bazochii; C. maesites* (ssp. *clenchi* probably was present in the Lesser Antilles but the refugium of *m. maesites* cannot be determined); *C. simaethis* (ssp. *jago* was probably present in the Jamaica refugium but the refugium of *s. simaethis* is not determinable.

In concluding this subject it may be of interest to add some observations on three related matters.

First, the Wisconsin extirpation of the Antillean lycaenids in Florida, the Bahamas, Puerto Rico and at least partially in Cuba, does not imply that these areas were without Lycaenidae during the glaciation. Florida, to judge by availability and systematic relations today, must have had a sizeable number of species; but which of these, if any, might have invaded the islands themselves is not known, nor is it ever likely to be since they have now all disappeared. From this last I should guess that the putative transient boreal element could not have been particularly large in the islands, or some would surely have managed somehow to survive into the present. A few species in other butterfly families, however, suggest just such a history. *Phyciodes phaon* Edwards (Nymphalidae) is a possible example.

Second, although it cannot be invoked in explanation of any known lycaenid distribution, the matter of altitudinal range deserves brief notice since it is definitely involved in the distribution of certain other butterflies. A species adapted to conditions found above an elevation of roughly 2000-2500 feet or so could have survived the suggested

glacial temperature drop more or less in place simply by moving downward. Such groups of species as *Calisto* (Satyridae), *Atlantea* (Nymphalidae),*Dismorphia* (Pieridae) and *Hymenitis* (Ithomiidae) probably owe their preservation through the Wisconsin glaciation to this factor.

Third, there are several groups of related species in the islands whose affinities suggest that they arose within the island area by a process analogous to that which has produced the now observable subspecies in many species. The Antillean species of *Electrostrymon* form one such group; the subgenus *Cyclargus* another; the Antillean *Allosmaitia* probably yet another. Each of these groups suggests dispersal through the islands from a refugium (or original beachhead of establishment in the islands) closely following a glacial recession. The degree of divergence in these instances and the subsequent history of several of the component species imply forcibly that a glaciation older than the Wisconsin was responsible, perhaps the next earlier (Illinoian).

2.   *Mainland colonization from the islands*

Under this heading I propose to unite the discussions of three different examples, all of which share the possibility that they have colonized the Central American mainland from the islands. This seems to be a novel idea: at least I know of no prior suggestion of it in any group. It is hard to tell though whether this is due to the probable rarity of the phenomenon or to such preoccupation with the many problems associated with invasion from the mainland that the idea of a reverse colonization simply never occurred to anyone. In any case there are three instances in the lycaenids where this seems to be indicated. Parenthetically it may be noted that of roughly 20 successful migrations between islands and mainland (other than Florida) needed to account for the Antillean Lycaenidae, three (15%) are of this abinsular type, the remaining 17 being more conventional adinsular colonizations. If the lycaenids represent a fair zoogeographic sampling of the island fauna, 15% is quite large enough to make abinsular colonizations worth looking for in other groups.

1.   *Strymon columella.* This species does not occur in South America but it is present in Central America (including Baja California and some of the offshore Pacific islands) where it ranges north into southern United States, and it occurs on all the major islands and island groups of the Greater Antilles. There are several related species in the West Indies (*antigua, toussainti, cristophei, limenia*), while in South America occur still other allied species. This pattern suggests that there was an early colonization of the Antilles, probably from South America, followed by speciation within the islands that resulted eventually in the formation of *columella.* Then, most likely during the Wisconsin, the latter crossed over into Central America. With

the recession of the Wisconsin sheet, in addition to spreading out from its island refugia it also spread, in Central America, to Baja California and to some of the islands off the West Coast.

The remaining two examples are even more unusual in that they show definite evidence of having come originally from Africa. So far I am aware these two, the *Leptotes marina* group and *Brephidium,* are the only New World Lycaenidae to which an African origin can be attributed. It has been suggested that *Zizula cyna* Edw. (purely continental from southern United States south to Brazil and Bolivia) is such an African derivative but fuller investigation does not support the contention. *Z. cyna* is a distinct New World species; its closest ally, the polytypic *Z. gaika* Trimen, ranges from Africa to Australia. Comparison of *cyna* with various *gaika* populations show a distinctly greater resemblance to those from eastern Asiatic localities than to those of Africa. The only conclusion possible on this evidence is that *cyna* was derived from Asia *via* the Bering Strait route and not from Africa.

2. *Leptotes marina* group. As pointed out above (note no. 7) this group consists of a number of species in Africa, Madagascar and several of the islands in the western Indian Ocean as well as the three New World species, *perkinsae* (Jamaica), *marina* (Central America) and probably *parrhasioides* Wallengren (Galapagos Islands).[5] The *marina* group occurs nowhere else but related groups also occur in Africa. The presence of members of the group on so many remote oceanic islands is dramatic evidence of a considerable propensity for colonizing across large water distances so it would be by no means impossible for a hypothetical *"marina* group ancestor" to have made the long voyage from Africa to the New World. The real question is the site of its landfall. On the face of it South America would appear to be the best answer by far; it is nearest to Africa and it is the largest available target for a random trajectory to hit. The evidence against this possibility, however, is to me persuasive though admittedly tenuous.

First, the present distribution of the New World members of the group is distinctly northern tropical, almost subtropical. Only *parrhasioides* is truly equatorial (in latitude but not in climate).

Second, for some unknown reason the tropics generally are not very favorable for the Plebejinae. This is least true in the East Indies, most true in the New World. It is therefore distinctly possible that a form of this subfamily arriving in eastern South America would be poorly equipped *a priori* to compete and establish itself there. In the West

[5]Comstock & Huntington (1943:95) cite *marina* from Chile and the Galapagos. It is hard to question the accuracy of such meticulous observers but it is even harder to accept these records. Either mislabelling or misdetermination would seem to be involved here.

Indies, on the other hand, conditions appear to be much more favorable to the subfamily. *Leptotes, Hemiargus* and *Pseudochrysops* flourish there and together make up a larger percentage of the lycaenid fauna than in any other tropical area in the Americas.

Third, comparison with *Brephidium* (which presents at least one additional type of evidence) shows a strongly similar pattern in many respects, and each thereby lends support to the other.

The tentative conclusion is that the ancester of the New World members of the *marina* group crossed from Africa to the West Indian region where it became established; that from there it successfully invaded the Central American mainland; and then spread from there to the Galapagos. It is impossible, at least with the information available now, to guess when this might have happened. Diversification of the group in the New World has left no tangible clues to evolution rates. One might say that if evolution rates in the group were more or less typical, then the Atlantic crossing might have been made in mid-Pleistocene or thereabouts but that is completely without documentation.

3. *Brephidium.* There are many points of similarity to the *marina* group in the distribution pattern of this genus, and just enough differences that, if they share a similar history, one tends to complement the other in evidence. There are three known species of *Brephidium* (omitting *B. barbouri* because of insufficient information):

B. pseudofea Morr., confined to Florida and Georgia with a single recently discovered colony (Rindge, 1952: 13) in the northern Bahamas.

B. exilis Bdv., widespread in the New World with these known and very distinct subspecies: nominate *exilis* from Oregon and Nebraska (probably not overwintering) south so far as now known to eastern Texas and on the Pacific Coast to southern Baja California and to Mazatlàn (Sinaloa, Mexico) at least; a still undescribed subspecies from coastal Yucatan; probably one or more other subspecies down to northern Venezuela, the limit of the known continental distribution of the species; *e. isophthalma* from the West Indies.

B. metophis Wallengren in South Africa, chiefly in the western Cape Province and western Orange Free State, more or less sympatric there with the related monotypic genus *Oraidium* (*barberae* Trimen). See Swanepoel (1953: 80-81) for information on these two species.

No other members of the genus and no other closely related genera are known anywhere.

The northern range of *exilis* on the mainland and its nearly complete absence from South America implies a northerly source, further supported by the presence of ssp. *isophthalma* in the Greater Antilles. The distinctness and the presence in Florida of *pseudofea* constitute strong presumptive evidence that it is there a survivor of an earlier invasion from the islands, again implying a longer occupancy by the genus in the Antilles than on the mainland, where only one species is known.

These points lead to the conclusion that an ancestral *Brephidium* crossed from Africa to the West Indies and became established there; then later spread to Florida to form *pseudofea;* and still later crossed to the mainland to give rise to the several subspecies of *exilis* now known there.

We are in a somewhat better position in *Brephidium* than in the *marina* group to date these events, however roughly. The presence of *isophthalma* on several Greater Antillean islands without apparent subspeciation is evidence that the evolution rate of *exilis* is rather low, requiring more than post-Wisconsin time to produce visible subspeciation. We are, therefore, led to conclude that the invasion of the mainland, where several distinct subspecies now occur (all different from the insular subspecies as well), preceded the Wisconsin; and that the origin of Floridian *pseudofea* must be much older still. The whole New World history of the genus could have been written since the onset of the Pleistocene, and may well have been, but it could easily have been even older.

In passing it may be noted that this suggestion of an African origin of New World *Brephidium* carries with it the likelihood that at the time of the Atlantic crossing *Brephidium* in Africa enjoyed a wider, or at least considerably different, range than it does now. Possibly it was then an inhabitant of the savanna regions of the interior of Upper Guinea.

3. *The Lesser Antilles fauna*

Our knowledge of the lycaenids of this curious chain of islands appears to be still fragmentary, but there are two points at least which warrant brief remarks and for which the distributional evidence seems adequate.

Mention has already been made of the likelihood that the Lesser Antilles served as a Wisconsin refugium. This refugium, however, appears to have functioned much less as a source of postglacial spreading than either of the other two primary refugia, Jamaica and Hispaniola. These facts are relevant: (1) the Virgin Islands are faunistically a part of the Lesser Antilles (cf. Comstock & Huntington, 1943: 121); (2) of the 12 lycaenid species regularly occurring in Puerto Rico, the first "port of call" for a potentially expanding Lesser Antillean refuge fauna, three (*C. maesites, C. simaethis, N. celida*) must be omitted for uncertainty of origin; three (*S. bubastus, H. hanno, H. woodruffi*) are clearly derived from the Lesser Antilles in postglacial times while the remaining nine are apparently derived from Hispaniola; (3) St. Kitts shares most, perhaps all, of its fauna with the Virgin Islands, but the remaining Lesser Antilles do not do so to the same extent. These three points suggest that the failure to expand postglacially may be more apparent than real. The problem would be neatly solved by making

the assumption that the Virgin Islands shared Puerto Rico's low temperatures during Wisconsin times and were therefore not inhabited; that when recession of the Wisconsin sheet began, invasion of Puerto Rico started from Hispaniola while simultaneously the Virgin Islands were being invaded from St. Kitts. This would explain not only the predominantly Hispaniolan character of the Puerto Rican fauna and the Lesser Antillean character of the Virgin Islands fauna but also the apparent failure of the Lesser Antillean refuge fauna to disperse; for under this hypothesis it would not have lacked capacity to disperse but simply did not have the opportunity to spread so far because of the opposing expansion of the Hispaniolan refuge elements.

Strikingly apparent is another aspect of this Lesser Antillean fauna: its integral relation to, and derivation from, the fauna of the Greater Antilles. Fourteen species are known from the islands, from the Virgin Islands to Grenada inclusive. Of this number one remains an enigma as to its origin (*S. rufofusca*); one is indeterminate and could have reached the Lesser Antilles from either the north or the south (*C. simaethis*); three are of unquestionable South American origin (*P. marsyas, S. bubastus, H. hanno*), and *L. c. cassius* may also have invaded the islands from South America as far as Martininque (only a single male is known from the island). The remaining nine species are of obvious Antillean derivation: *A piplea, S. acis, S. antigua, E. angelia, E. angerona, E. dominicana* (probably), *C. maesites, H. woodruffi, L. cassius* (sspp. *catalina* and *chadwicki*). Counting only those of reasonably assured origin shows that the Lesser Antillean fauna is about 75% Greater Antillean in origin, 25% South American.

4. The age of the Antillean lycaenid fauna

Throughout the preceding discussion attempt has been made wherever possible to apply some sort of age estimate to the events set forth. By extending analogous reasoning as well to species not specifically discussed we reach an interesting conclusion concerning the age of the lycaenid fauna now in the Antilles. At least two glaciations are required for certain species groups (*Brephidium, Electrostrymon, Cyclargus*); no member of the fauna is so remote systematically from its nearest continental ally that the differentiation could not have occurred since the onset of the Pleistocene. One may conclude from this that early Pleistocene, more or less, is the most likely time for the initiation of events that culminated in today's fauna. If evolution rates were substantially less than is here estimated, then of course this time would need to be pushed back accordingly.

In brief there is no firm evidence of the time this fauna first began to invade the islands, but contributing data in the form of systematic affinities and suggested or implied evolution rates in "typical" lines lead to the conclusion that early Pleistocene is the most likely time.

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